



Review

Plant-biotic interactions under elevated CO₂: A molecular perspectiveKemal Kazan^{a,b,*}^a Commonwealth Scientific and Industrial Research Organisation (CSIRO) Agriculture and Food, Queensland Bioscience Precinct, Brisbane, Queensland, Australia^b Queensland Alliance for Agriculture & Food Innovation (QAAFI), The University of Queensland, Brisbane, Queensland, Australia

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ABSTRACT

Elevated levels of atmospheric CO₂ are predicted to contribute to major climatic changes during the next 50–100 years. This can have a significant impact on future food security if such changes make crop plants vulnerable to biotic and abiotic stresses. Indeed, a growing body of recent studies highlighted in this review show that elevated CO₂ (eCO₂) directly and/or indirectly influence plant-biotic interactions. In many instances, eCO₂ alters phytohormone and reactive oxygen signalling, secondary metabolism as well as defence-associated development such as stomatal responses in the host. eCO₂ can also directly and/or indirectly influence pathogenesis- and herbivory-related traits in pest and pathogen populations although currently very little is known about the molecular mechanisms involved in such effects. In addition, eCO₂ alters predator-prey interactions by interfering with indirect defences and chemical communications in insect pests. A better understanding of molecular mechanisms involved in plant-biotic interactions under eCO₂ will be critical towards mitigation of potentially adverse effects of climate change on crop production.

1. Introduction

Climate change is a global challenge that will have an increasingly noticeable impact on many facets of human, animal and plant life in the near future. Because crop production is heavily dependent on climatic conditions, radical changes predicted to occur in the world's climate have the potential to threaten future food security. In particular, major changes in global temperatures and rainfall patterns can make crop plants vulnerable to biotic (pests, pathogens, weeds and parasitic plants) and abiotic (cold, high light, ozone, nutrients and drought) stresses (Ahuja et al., 2010; Bebbler, 2015; Bregaglio et al., 2013; Chakraborty and Newton, 2011; DeLucia et al., 2008, 2012; Elad and Pertot, 2014; Fones and Gurr, 2017; Gautam et al., 2013; Gregory et al., 2009; Juroszek and von Tiedemann, 2013; Luck et al., 2011; Pautasso et al., 2012; Reddy, 2013; Vaughan et al., 2016a). Indeed, a growing body of evidence indicates that climate change alters pest and pathogen resistance by altering the physiology, morphology, nutritional status,

and/or defence responses of plant hosts (Bebbler, 2015; Jones, 2016; Jones and Barbetti, 2012; Trebicki et al., 2017a). In addition, climate change can directly and/or indirectly affect the distribution, abundance, activity, fitness, behaviour, aggressiveness, host specificity and the ability to survive under extreme conditions of pests and pathogens (Neher et al., 2004; Xie et al., 2015a; Ziska and McConnell, 2016). Furthermore, a changing climate may require the adoption of certain agricultural practices that directly or indirectly influence plant-parasite interactions (Furlong and Zalucki, 2017). For instance, minimum tillage and stubble retention increasingly used to conserve soil moisture in dry regions promote the incidence of soil-borne diseases (Kazan and Gardiner, 2018). However, it is also possible that certain current pest and pathogen problems might lose their importance under climate change. Therefore, a better understanding of how plants interact with their biotic environment is essential to minimise climate change-related crop losses in the future.

eCO₂ is the major driver of climate change. In parallel to

Abbreviations: ABA, abscisic acid; ACC-S, amino-cyclopropane-1-carboxylate synthase; aCO₂, ambient CO₂; AOS1, ALLENE OXIDE SYNTHASE1; APR, *Acyrtosiphon pisum* Resistance; BYDV, Barley Yellow Dwarf Virus; C/N ratio, Carbon/nitrogen ratio; CGA, chlorogenic acid; CMV, Cauliflower Mosaic Virus; COR, coronatine; CRSP, CO₂ Responsive Secreted Protease; CysPI, cysteine protease inhibitor; DON, deoxynivalenol; eCO₂, elevated CO₂; EPF2, Epidermal Patterning Factor2; ETI, Effector-Triggered Immunity; Eβf, (E)-β-farnesene; FACE, Free Air CO₂ Enrichment; HCO₃⁻, carbonate; HSP90, HEAT SHOCK PROTEIN90; ICS1, ISOCHORISMATE SYNTHASE1; IPCC, Intergovernmental Panel on Climate Change; JA, jasmonate; JAR1, JASMONATE RESISTANCE1; ICO₂, low CO₂; LOX, lipoxygenase; MAPK, mitogen activated protein kinase; NO, nitric oxide; NPR1, NONEXPRESSER OF PR GENES1; NR, nitrate reductase; NRB4/MED15, NON-RECOGNITION-OF-BTH4/MEDIATOR15; OST1, OPEN STOMATA1; PAMPs, Pathogen Associated Molecular Patterns; *Pst*, *Pseudomonas syringae* pv. *tomato*; PTI, PAMP-triggered immunity; R, resistance gene; Rboh, respiratory burst oxidase homolog; ROS, reactive oxygen species; SA, salicylic acid; SLAC1, Slow Anion Channel Associated1; TMV, tobacco mosaic virus; TYLCV, Tomato yellow leaf curl virus; VOCs, volatile organic compounds; ZA4, zealexin A4; βCA, β-carbonic anhydrase

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industrialisation and deforestation, atmospheric CO₂ levels went up from 280 ppm to 400 ppm in the last century, and are predicted to reach 730–1000 ppm towards the end of this century (IPCC, 2014; Meehl et al., 2007). It is becoming increasingly evident that eCO₂, apart from its causative role in climate change, can have a variety of direct and indirect effects on crop production. Although positive effects of eCO₂ on crop production (C3 plants in particular) are known, such effects are largely dependent on the availability of water and nutrients and were mostly assessed in the absence of stresses (AbdElgawad et al., 2016; Becklin et al., 2017; Ghini et al., 2015; Gray and Brady, 2016).

The effect of eCO₂ on plant health can vary from detrimental to neutral and even beneficial, depending on the type of plant-parasite interactions. In many instances, eCO₂ can directly and/or indirectly alter various components of host and parasite biology during plant-biotic interactions (Górial et al., 2013; Jwa and Walling, 2001; Kobayashi et al., 2006; McElrone et al., 2005; Sharma et al., 2016; Váry et al., 2015; Xie et al., 2015b; Zavala et al., 2012, 2013). However, any known effects of eCO₂ on plant-parasite interactions occur in a quantitative manner. To the best of my knowledge, there has not been any example where eCO₂ converts an incompatible plant-pathogen interaction to a compatible one or vice versa.

It is expected that a better understanding of molecular events regulated by eCO₂ during plant-parasite interactions will lead to the development of crop cultivars better adapted to adverse effects imposed by a changing climate. Towards this aim, recent studies that revealed mechanistic insights into the role of eCO₂ in plant-biotic interactions are briefly highlighted in this paper. The term “biotic” used in the paper broadly refers to plant pathogenic bacteria, viruses, fungi as well as herbivorous and sap-sucking insects such as aphids. Most studies reviewed in this paper have used 700–800 ppm of CO₂ concentrations as eCO₂ treatments and therefore unless indicated otherwise, the term “eCO₂” used here refers to CO₂ concentrations at this range.

2. CO₂ sensing mechanisms in plants

Given the importance of CO₂ in photosynthetic carbon fixation, plants have developed sophisticated mechanisms to sense and respond to CO₂. The stomata are specialised organs involved in gas exchange, mainly the intake of CO₂, which is required for photosynthesis, and the release of O₂ and water vapour. eCO₂ promotes stomatal closure and inhibits stomatal re-opening (Assmann, 1993). eCO₂ also reduces stomatal densities (reviewed by Mizutani and Kanaoka, 2017). βCA1 and βCA4, the two β-carbonic anhydrase enzymes found in stomatal guard cells, play critical roles in CO₂ sensing (Engineer et al., 2014; Hu et al., 2010; Mizutani and Kanaoka, 2017). βCAs catalyse the conversion of CO₂ to HCO₃⁻ (carbonate) required for the protein kinase OST1 (OPEN STOMATA1). OST1 regulates the expression of S-type anion channels functioning in CO₂-dependent stomatal closure (Xue et al., 2011). HCO₃⁻ is also required for the induction of CRSP (CO₂ Responsive Secreted Protease) and EPF2 (Epidermal Patterning Factor2) encoding major players involved in stomatal development. The CRSP-mediated cleavage of pre-EPF2 peptides activates EPF2, which in turn binds to the ERECTA receptor kinase, a known suppressor of stomatal development (Fig. 1) (reviewed by Mizutani and Kanaoka, 2017) as well as a regulator of disease resistance (Häffner et al., 2014).

Plant stomatal responses are regulated by phytohormones and reactive oxygen species (ROS) as well as by pathogens and herbivores (Daszkowska-Golec and Szarejko, 2013; DeLucia et al., 2012; Meza-Canales et al., 2017; Murray et al., 2016; Shi et al., 2015), indicating possible integration of CO₂-mediated developmental and physiological responses into pathways regulating disease resistance. Currently very little is known how this integration is achieved molecularly. However, new research suggests possible interactions between defence and CO₂-sensing pathways in plants. For instance, both SA and SA signalling components NPR1 (NONEXPRESSOR OF PR GENES1) and NRB4/MED15 (NON-RECOGNITION-OF-BTH4/MEDIATOR15) physically

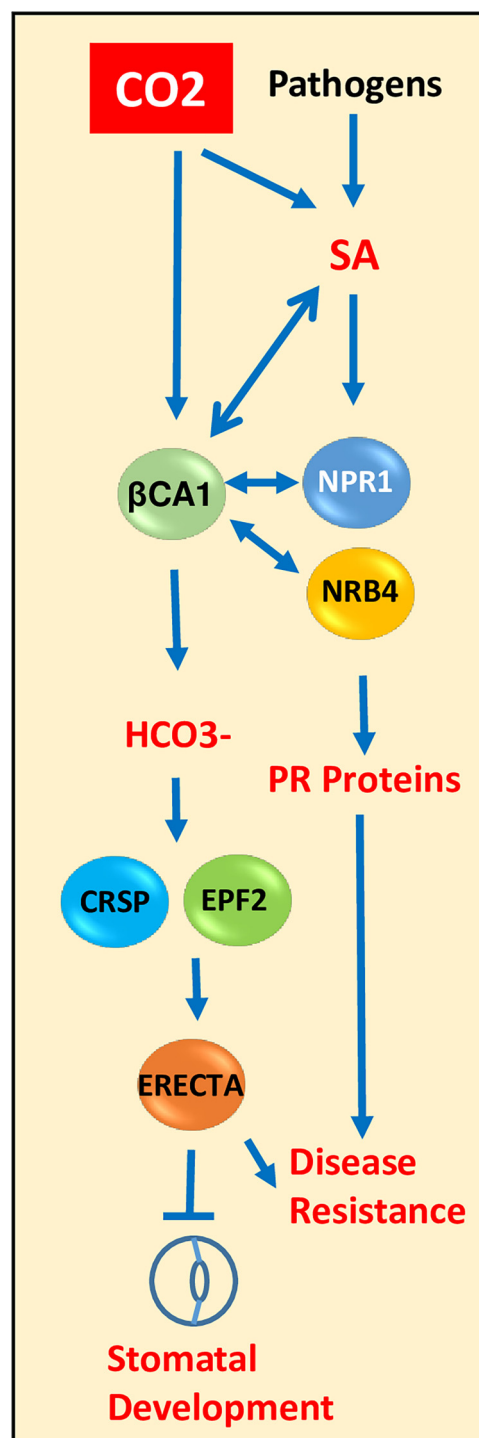


Fig. 1. Crosstalk between CO₂ sensing and the SA pathway in Arabidopsis. CO₂ is sensed by guard cell located β carbonic anhydrases (βCAs) that catalyse the conversion of CO₂ into HCO₃⁻ (carbonate). This initiates a signalling pathway that impinges on the ERECTA kinase which inhibits stomatal development. eCO₂ also activates SA biosynthesis and signalling. Both SA and SA signalling components NPR1 and NRB4 regulating the expression of PR (Pathogenesis Related) genes physically interact with βCA1, suggesting that a link might exist between CO₂ and SA sensing. The ERECTA kinase involved in stomatal development is also a known regulator of disease resistance.

interact with βCA1 (Medina-Puche et al., 2017), suggesting a potential link between SA-mediated defence and stomatal responses to CO₂ (Fig. 1). Indeed, the SA pathway has been implicated in stomatal closure (reviewed by Panchal and Melotto, 2017) and βCA mutants

compromised in CO₂ sensing display aberrant SA perception phenotypes (Medina-Puche et al., 2017).

ABA is another phytohormone that regulates biotic and abiotic stress responses in plants (Kazan and Lyons, 2014). Both ABA as well as ABA signalling (e.g. ABA perception) are required for CO₂-mediated stomatal responses in Arabidopsis (Chater et al., 2015). In contrast, jasmonates (JAs) and JA signalling are required for eCO₂-mediated stomatal closure in *Brassica napus* as ABA levels do not change under eCO₂ in this species (Geng et al., 2016). Several JA signalling mutants such as *jin1/myc2* (Kazan and Manners, 2013) show altered stomatal responses under eCO₂ in Arabidopsis (Geng et al., 2016).

As indicated above, ROS (H₂O₂ and NO) are also critical signals for both stomatal and defence responses in plants (Sewelam et al., 2016; Shi et al., 2015). To regulate stomatal closure, eCO₂ promotes ROS formation in stomatal guard cells through the action of plasma membrane NADPH oxidases (Chater et al., 2015). Indeed, loss-of-function mutants of the Arabidopsis NADPH oxidase encoding genes *RbohD* and *RbohF* show attenuated stomatal responses under eCO₂ (Chater et al., 2015). Furthermore, the ability to induce ROS in response to eCO₂ is compromised in the triple ABA receptor mutant *pyr1 pyl1 pyl4*, suggesting that ABA perception is required for ROS formation (Chater et al., 2015). The involvement of ROS and phytohormones in both stomatal and defence responses suggest the existence of an interplay between these pathways and eCO₂ during plant-biotic interactions. Readers interested in detailed aspects of CO₂ sensing and stomatal development are referred to other reviews (Engineer et al., 2016; McLachlan et al., 2014; Mizutani and Kanaoka, 2017).

3. CO₂ sensing mechanisms in fungi and insects

Plant pathogenic fungi and insect pests are non-photosynthetic or heterotrophic and thus rely on the carbon fixed by the host plant. Although, the mechanisms involved in CO₂ sensing in the model fungus yeast and fungal animal pathogens such as *Cryptococcus neoformans* have been described (Bahn et al., 2005; Bahn and Mühlischlegel, 2006; Cottier et al., 2012, 2013), it is mostly unclear if plant pests and pathogens have the ability to directly sense the changes in atmospheric CO₂ concentrations and if so, how this would affect pathogenesis- or herbivory-related processes in these organisms. Interestingly, the roles of carbonic anhydrases in CO₂ sensing appear to be conserved in fungi. For instance, HCO₃⁻ produced by fungal carbonic anhydrases activates an adenyl cyclase that regulates various metabolic and developmental processes in *C. neoformans* and yeast (reviewed by Martin et al., 2017; Mogensen et al., 2006). Therefore, it can be speculated that similar CO₂ sensing mechanisms operate in both plants and pathogenic fungi.

In *Drosophila* (*Drosophila melanogaster*), two chemosensory receptors are involved in CO₂ sensing (Jones et al., 2007). Similar receptors are also found in other insect species, including the agriculturally important herbivorous insect cotton bollworm (*Helicoverpa armigera*) (Ning et al., 2016; Xu and Anderson, 2015). The CO₂ released from maize roots acts as a volatile signal that attracts the larvae of the western corn rootworm *Diabrotica virgifera virgifera* (Rodrigues et al., 2016). The genes encoding CO₂ receptors are highly expressed in this insect, suggesting that CO₂ sensing might be important for herbivory. However, it is mostly unknown if eCO₂ directly influences pathogenesis- and/or herbivory-related processes in this or other insect species. Nevertheless, eCO₂ seems to directly influence insect development as the effect of eCO₂ on various developmental traits of *H. armigera* while feeding on an artificial diet has been observed (Akbar et al., 2016).

4. eCO₂ and stomatal responses during plant-biotic interactions

Various leaf infecting pathogens enter the host through stomatal openings and thus plants close their stomata to restrict pathogen infections (Melotto et al., 2017). Pathogen-derived molecules such as oligogalacturonic acid and chitosan, a component of plant and fungal

cell walls, respectively, as well as the fungal toxin fusaric acid elicit stomatal closures (reviewed by Lake and Wade, 2009). However, some pathogens have developed strategies to manipulate host stomatal responses (Grimmer et al., 2012). For instance, the bacterial pathogen *Pseudomonas syringae* pv. *tomato* (*Pst*) employs coronatine (COR), a toxin and a JA analog, to force stomata reopen during infection (Melotto et al., 2017).

Given the well-established roles of eCO₂ in reducing stomatal apertures and density, it is expected that eCO₂ alters the interaction between plants and the pathogens that infect via stomata (Chater et al., 2015). Indeed, tomato plants show reduced stomatal apertures and increased resistance to *Pst* when grown under eCO₂ (Li et al., 2015), suggesting that eCO₂-mediated stomatal closure is a mechanism that restricts pathogen entry into leaves. In Arabidopsis, eCO₂ does not alter the way that Arabidopsis stomata close rapidly within an hour in response to *Pst* as the same response is also seen under lowCO₂ (lCO₂) and ambient (aCO₂) (Zhou et al., 2017). However, COR-induced stomatal reopening at 4 h following infection occurs only under aCO₂ and eCO₂ but not at lCO₂ (150 ppm). Consequently, Arabidopsis show increased resistance to *Pst* under lCO₂. In addition, increased *Pst* resistance correlates with reduced ABA levels (Zhou et al., 2017). Indeed, the ABA deficient Arabidopsis mutant *aba2* shows an attenuated response to COR-mediated stomatal reopening (Zhou et al., 2017). The stomatal closure in tomato is also correlated with elevated levels of nitric oxide (NO) produced in stomatal guard cells under eCO₂ (Fig. 2A). Silencing of the genes encoding a nitrate reductase (NR) and a guard cell slow anion channel 1 (SLAC1; Slow Anion Channel Associated1) involved in NO production, abolishes eCO₂-mediated stomatal closure and leads to increased infections by *Pst* (Li et al., 2015). However, despite affecting stomatal closures, SLAC1-mediated *Pst* resistance is not entirely dependent on NO. SLAC1-silenced plants still show reasonable levels of *Pst* resistance under eCO₂, suggesting that eCO₂-mediated resistance to *Pst* involves both stomatal- and non-stomatal defences (Li et al., 2015). Indeed, when syringe inoculation is used to bypass stomatal defences and deliver the bacteria directly into intracellular spaces, tomato plants grown under eCO₂ retain their *Pst* resistance (Li et al., 2015).

Host stomatal responses can also be effective against xylem-feeding insects. For instance, the pea aphid *Acyrtosiphon pisum* induces stomatal closures in *Medicago truncatula* in an ABA-dependent manner (Sun et al., 2015). This host response is thought to be beneficial to the aphid because stomatal closure reduces transpiration-mediated water losses and improves leaf water status. These physiological responses, in turn, promote xylem feeding by the aphid for extended periods (Fig. 2B). eCO₂ also induces the expression of the mitogen activated protein kinase (MAPK) MPK4, which increases the feeding efficiency of the green peach aphid *Myzus persicae* by differentially regulating stomatal responses and JA-dependent defences in *Nicotiana attenuata* (Fig. 2C) (Guo et al., 2017). Similarly, the aggressiveness of *Erysiphe cichoracearum*, a biotrophic fungal pathogen that causes powdery mildew on Arabidopsis, increases under eCO₂. This increase is correlated with altered epidermal features of the host such as increased stomatal densities, guard cell lengths and trichome numbers (Lake and Wade, 2009). Stomata also play a role in insect resistance by regulating volatile emissions that can attract the enemies of attacking insects (Seidl-Adams et al., 2015; see also below).

Mutant analyses in Arabidopsis suggest that stomatal closure observed under eCO₂ is not directly associated with the induction of defence responses. It was proposed that the effect of eCO₂ on plant defence occurs indirectly and is partially associated with an increased metabolic activity and redox signalling. Supporting evidence for this view comes from the experiments where the inhibition of glutathione content or NADPH generating enzymes block the priming of SA-dependent defences and associated pathogen resistance (Mhamdi and Noctor, 2016).

In addition to stomatal responses, various developmental alterations

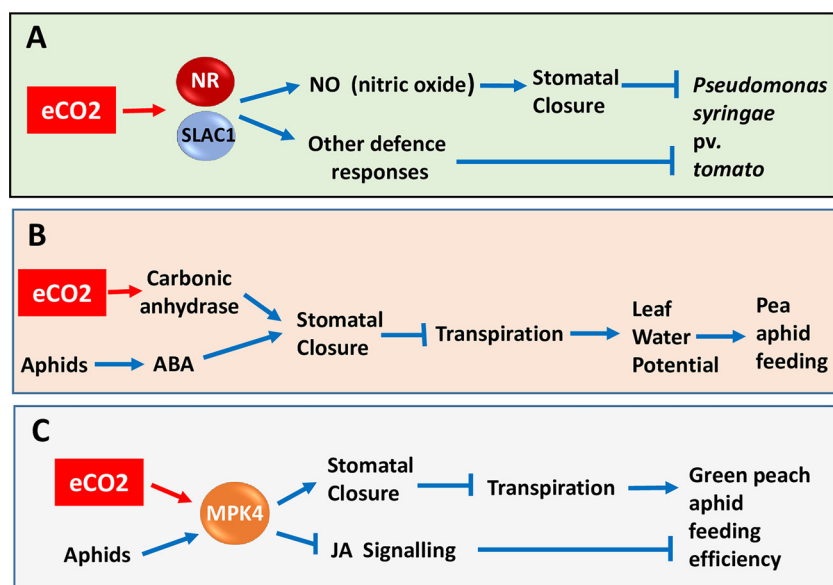


Fig. 2. Elevated CO₂ (eCO₂) modulates stomatal responses during plant-parasite interactions.

A) eCO₂ promotes nitric oxide (NO) production in stomatal guard cells through NR (NITRATE REDUCTASE) and SLAC1 (SLOW ANION CHANNEL ASSOCIATED1) to induce stomatal closure which then restricts the entry of the bacterial pathogen *Pseudomonas syringae* pv. *tomato* into tomato leaves (Li et al., 2015). **B)** eCO₂ and aphid feeding promote stomatal closure through a carbonic anhydrase and ABA signalling. This reduces transpiration mediated water losses and increases the feeding efficiency of the green peach aphid *Acyrtosiphon pisum* (Sun et al., 2015). **C)** eCO₂ and aphid feeding induces MPK4-mediated stomatal closure in *Nicotiana attenuata* to reduce transpiration-mediated water losses. This improves leaf water status and promotes the feeding efficiency of the green peach aphid *Myzus persicae*. MPK4 (MAP KINASE 4) also attenuates JA signalling required for aphid resistance (Guo et al., 2017).

caused by eCO₂ in the host plant can affect the outcome of plant-biotic interactions. For instance, eCO₂-induced increase in plant canopy may provide a microclimate that promotes the infection by the anthracnose fungus *Colletorichum gleosporoides* (Chakraborty and Datta, 2003). In *M. truncatula*, the ability to fix nitrogen influences host developmental responses such as trichome densities, which in turn affect epidermal resistance to aphids under eCO₂ (Guo et al., 2014).

5. eCO₂ and plant defence signalling

Phytohormone signalling pathways play important roles in regulating plant defence. In the following sections, the effect of eCO₂ on defence signalling regulated by the major defence hormones SA and JA as well their crosstalk will be briefly reviewed.

5.1. eCO₂ and SA signalling

Salicylic acid (SA) is one of the phytohormones with major defensive roles, particularly against biotrophic fungal pathogens and phloem-feeding insects. SA activates a subset of defence genes encoding pathogenesis-related proteins (e.g. *PR1*). Under eCO₂, SA levels increase in tobacco (Matros et al., 2006), soybean (Casteel et al., 2012a) tomato (Huang et al., 2012; Zhang et al., 2015) as well as in Arabidopsis, bean (*Phaseolus vulgaris*) and wheat (*Triticum aestivum*) but not in barley (*Hordeum vulgare*) (Mhamdi and Noctor, 2016), suggesting this is a species-specific response. In Arabidopsis, elevated SA levels observed following the transfer of plants into an eCO₂ environment slowly return to basal levels after four days. This observation has led to the suggestion that transient increases observed in SA levels could be due to a shock caused by eCO₂ rather than a sustained effect mediated by eCO₂ (Mhamdi and Noctor, 2016). Nevertheless, in Arabidopsis, eCO₂ triggers the expression of the *ISOCHORISMATE SYNTHASE1* (*ICS1*) encoding a SA biosynthesis enzyme and SA-responsive defence genes *PR1*, *PR2* and *PR5*. In addition, JA levels and the expression of JA-responsive defence genes such as *PAD3*, *LOX3*, *OPR3*, *JAZ10* and *PDF1.2* increase under eCO₂ (Mhamdi and Noctor, 2016). The concomitant activation of SA and JA pathways leads to increased resistance to both *Pst* and the necrotrophic fungal pathogen *Botrytis cinerea* in Arabidopsis (Mhamdi and Noctor, 2016; Fig. 3A). However, the activation of the SA pathway by eCO₂ seems to have negative consequences on plant growth. In the absence of pathogen threat, the Arabidopsis SA-deficient *sid2* mutant produces a larger rosette under eCO₂ than wild-type plants (Mhamdi and Noctor, 2016).

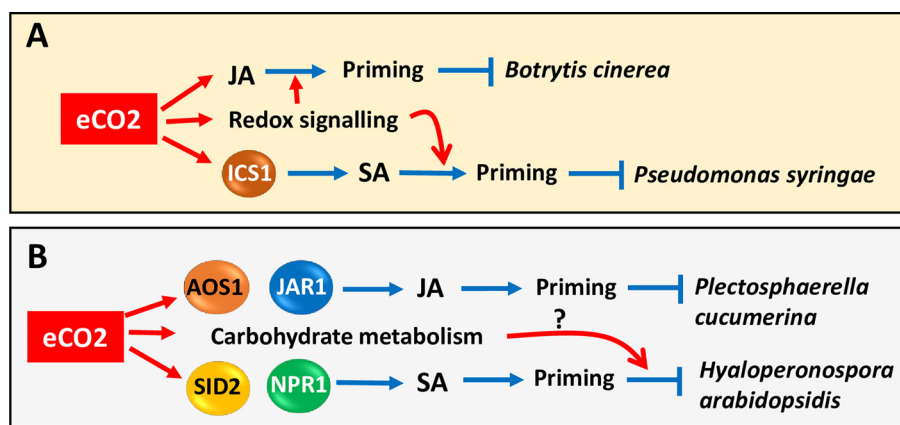
The actual mechanism of how eCO₂ alters the SA pathway is not clear. However, it was argued that the effect of eCO₂ on the SA pathway could be linked to the inhibitory effect of eCO₂ on photorespiration, which primes plant defence through its effect on ROS production (Noctor and Mhamdi, 2017). The link stated above between CO₂-sensing mechanisms and SA responses might also have a role in this phenomenon (Fig. 1).

5.2. eCO₂ and JA signalling

The JA signalling pathway confers resistance to necrotrophic fungal pathogens and chewing insects while some pathogens have evolved to exploit this pathway to cause disease (Kazan and Lyons, 2014; Thatcher et al., 2009). Therefore, several studies have examined the effect of eCO₂ on JA signalling to determine if altered disease development observed under eCO₂ could be linked to JA signalling. Emerging evidence indicates that eCO₂ negatively affects the JA pathway during various plant-parasite interactions. For instance, the majority of soybean cultivars challenged in the field with the Japanese beetle (*Popillia japonica*) shows reduced JA levels under eCO₂.

However, not all soybean cultivars examined exhibits this response, indicating that plant genotype plays a role in the regulation of JA-dependent defences under eCO₂ (Casteel et al., 2012a). This latter study did not investigate whether eCO₂-mediated suppression of the host JA pathway promotes herbivory in soybean. However, the availability of genetic variation for this trait indicates the possibility that soybean genotypes that do not show compromised JA-responses under eCO₂ can be used in breeding programs to eliminate the negative effects of eCO₂ on JA-dependent defences.

JAs synthesised through the lipoxygenase (LOX) pathway are required for caffeine, a purine alkaloid involved in plant defence, -mediated disease resistance against *C. gloeosporioides*, a fungal pathogen that causes the brown blight disease in tea (*Camellia sinensis* L.) (Li et al., 2016). Under eCO₂, endogenous JA and caffeine levels are reduced while the susceptibility of tea plants to *C. gloeosporioides* is increased, suggesting that eCO₂-mediated suppression of caffeine is responsible for increased disease susceptibility (Fig. 4A) (Li et al., 2016). Similarly, in tomato, eCO₂ suppresses both JA levels and the expression of proteinase inhibitor encoding genes *PI I* and *PI II*, leading to increased susceptibility to *B. cinerea* (Fig. 6A) (Zhang et al., 2015). In *M. truncatula*, eCO₂ negatively regulates the JA pathway effective against the pea aphid *Acyrtosiphon pisum*. This response enables the aphid to feed on the plant for longer periods and gain increased weight



INDUCTION DEFICIENT 2) and NPR1 (NONEXPRESSER OF PR GENES 1) are required for SA-mediated priming (Williams et al., 2018).

(Guo et al., 2014). eCO₂ suppresses JA-dependent production of defence related molecules effective against the cotton bollworm in tomato (Guo et al., 2012) (Fig. 4C). eCO₂ also compromises JA-dependent induction of defence genes, the production of secondary metabolites and volatile organic compounds (VOCs) and thereby reduces resistance against the root-knot nematode *Meloidogyne incognita* in tomato (Sun et al., 2011) (Fig. 4D).

Interestingly, positive effects of eCO₂ on JA-dependent defences have also been reported, suggesting that the effect of eCO₂ on JA responses can be host- and/or attacker-dependent. For instance, eCO₂ positively regulates the JA pathway and the levels of various JA-induced metabolites during herbivory by the lepidopteran insect *Spodoptera litura* in tobacco and this reduces the biomass of the feeding insect (Lu et al., 2018) (Fig. 4B). In contrast, eCO₂ attenuates the induction of the JA pathway and JA-associated defensive metabolites in rice and this results in an increased weight gain of another lepidopteran insect pest *Mythimna separate* (Lu et al., 2018) (Fig. 4B).

Finally, the effect of eCO₂ on the JA pathway seems to be dependent

on the existing levels of JA-dependent defences. eCO₂ suppresses JA-dependent defence against root-knot nematode (*M. incognita*) in a so-called “defence-dominant genotype” that expresses a *35S:Prosystemin* construct, constitutively activating JA-dependent defences. However, no such suppression could be observed in wild-type and the *spr2* (suppressor of prosystemin-mediated responses2) mutant deficient in JA-dependent defences (Sun et al., 2011).

5.3. eCO₂ and hormonal crosstalk

The upregulation of the SA pathway providing resistance to various biotrophic fungi as well as bacterial pathogens and viruses could be a beneficial outcome of eCO₂. However, the existence of antagonistic interactions between SA and JA pathways (Kazan and Manners, 2008) means that SA-mediated pathogen resistance could attenuate JA signalling and increase the susceptibility to certain other parasites (mostly fungal necrotrophs and insects) that are sensitive to JA-regulated defences. For instance, eCO₂ enhances the SA pathway while suppressing

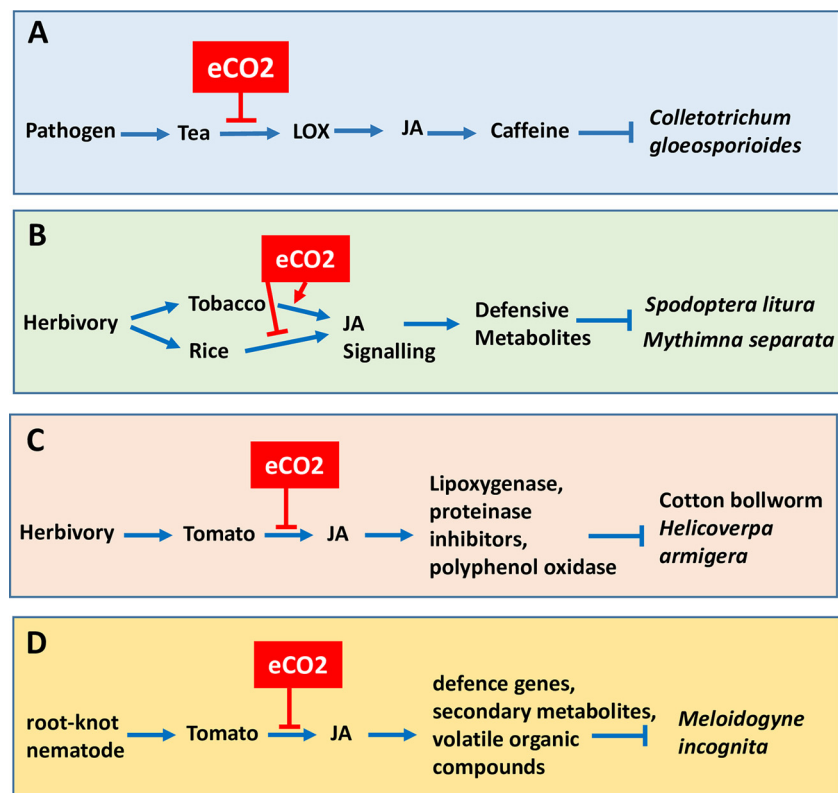


Fig. 4. eCO₂ modulates JA signalling and JA-mediated production of defence compounds during host-parasite interactions.

A) In tea, eCO₂ suppresses JA-mediated activation of caffeine involved in conferring resistance to the fungal pathogen *Colletotrichum gloeosporioides*. LOX (Lipoxygenase) (Li et al., 2016).

B) eCO₂ differentially regulates JA-mediated production of defensive metabolites effective against insects in tobacco and rice (Lu et al., 2018).

C) eCO₂ suppresses JA-dependent production of defence related molecules effective against the cotton bollworm in tomato (Guo et al., 2012).

D) eCO₂ suppresses root-knot nematode (*Meloidogyne incognita*) induced JA signalling and the production of JA-associated metabolites that confer increased nematode resistance in tomato (Sun et al., 2013).

the JA pathway in *Arabidopsis* and this results in an increased abundance of the peach aphid *Myzus persica* (Sun et al., 2013). Similarly, eCO₂ promotes endogenous SA levels while reducing JA levels in tomato. This increases *Pst* and TMV (tobacco mosaic virus) resistance while reducing *B. cinerea* resistance in a manner that is dependent on NPR1, a major regulator of the crosstalk between SA and JA signalling (Kazan and Manners, 2008). In *npr1*-silenced plants, *PI I* and *PI II* transcript levels as well as *B. cinerea* resistance increase under eCO₂, suggesting that eCO₂ promotes SA-JA antagonism in this species (Fig. 6A) (Zhang et al., 2015).

In contrast to the tomato-*Pst* interaction, where eCO₂ up- and down-regulates SA and JA pathways, respectively, in *Arabidopsis*, eCO₂ simultaneously upregulates both SA and JA signalling, resulting in enhanced resistance to both *Pst* and *B. cinerea* (Fig. 4A) (Mhamdi and Noctor, 2016). This latter observation seems to be inconsistent with the view that SA and JA pathways act in a mutually antagonistic manner (Kazan and Manners, 2008). However, it was speculated that the intracellular oxidative stress experienced by the plant during growth under eCO₂ might be responsible for the activation of both pathways (Mhamdi and Noctor, 2016). Similarly, eCO₂ positively influences both SA and JA levels as well their signalling pathways in mustard (*Brassica juncea*) and these alterations correlate with increased disease resistance against the necrotrophic fungal pathogen *Alternaria brassicae* (Mathur et al., 2018).

6. eCO₂ and R-gene mediated defence

Plants sense the presence of a pest or a pathogen by detecting conserved pathogen-associated molecules known as Pathogen Associated Molecular Patterns (PAMPs) through extracellular Pattern Recognition Receptors (PRRs). Pathogen detection results in the activation of host defences and increased resistance to pests and pathogens. This phenomenon is known as PAMP-triggered Immunity or PTI (Kazan and Lyons, 2014). Pests and pathogens also produce specific effectors recognised directly or indirectly by plant disease resistance (R) genes. Pathogen recognition activates R-gene dependent defence responses, often leading to a state of complete immunity known as Effector-Triggered Immunity or ETI (Kazan and Lyons, 2014).

In the model legume *M. truncatula*, the presence a R gene conferring resistance to the pea aphid *A. pisum* influences the way that this plant species responds to aphid attack under eCO₂. The resistant isogenic line Jester containing the R gene APR (for *Acyrtosiphon pisum* Resistance) shows stronger expression of defence genes than the susceptible isogenic line A17 under eCO₂. Interestingly, eCO₂ differentially regulates different defences in the resistant and susceptible isogenic lines. For instance, PTI-related defences, including the SA pathway, are elevated in the susceptible line A17 under eCO₂. In contrast, eCO₂ promotes ETI-related defences, while suppressing PTI-defences, in the resistant genotype Jester. In A17, eCO₂ also suppresses JA signalling, which is

known to be effective against aphids, leading to increased aphid feeding (Fig. 5A). Furthermore, HSP90 (HEAT SHOCK PROTEIN90), a chaperone protein involved in R gene-mediated disease resistance, is needed for this response as the silencing of *HSP90* impairs disease resistance in Jester (Fig. 6B) (Johnson and Züst, 2018; Sun et al., 2018).

Similarly, the presence of the *Mi-1.2* gene conferring resistance to nematodes and sap-sucking insects such as *Bemisia tabaci* (whiteflies) that transmits *Tomato yellow leaf curl virus* (TYLCV) determines the way that tomato plants respond to virus infection. eCO₂ increases TYLCV resistance in Moneymaker, a tomato cultivar not containing the *Mi-1.2* resistance gene, and this increase in resistance is correlated with elevated SA responses. In contrast, eCO₂ reduces TYLCV resistance in *Mi-1.2* plants by suppressing the SA pathway (Guo et al., 2016). In either case, no effect of eCO₂ on whiteflies as a vector transmitting the virus was found, suggesting that the observed effects of eCO₂ are most likely due altered plant defences (Guo et al., 2016).

7. eCO₂ and defence priming

The so-called “priming” response triggered by a previous exposure to a biological or chemical agent that stimulates host defences plays an important role in plant immunity as primed plants respond to pathogen infection in a faster and stronger manner than non-primed plants (Conrath, 2011). In *Arabidopsis*, eCO₂ (1200 ppm) enhances resistance to the necrotrophic fungal pathogen *Plectosphaerella cucumerina* by priming JA-dependent defences when disease development is assessed in a manner that takes the growth promoting effects of eCO₂ into consideration (Williams et al., 2018). This effect requires ALLENE OXIDE SYNTHASE 1 (AOS1) and JASMONATE RESISTANCE 1 (JAR1), the two enzymes involved in JA biosynthesis (Fig. 3B). In *Arabidopsis*, eCO₂ promotes resistance to the oomycete pathogen *Hyaloperenospora arabidopsidis*, at least in part through primed SA-dependent defences and altered host carbohydrate metabolism (Fig. 3B) (Williams et al., 2018).

8. eCO₂ and host secondary metabolism

Secondary metabolites produced in plants in response to pest and pathogen attack play important roles in defence. One of the ways that eCO₂ influences biotic interactions is through the regulation of secondary metabolites including phytoalexins (Braga et al., 2006; Hartley et al., 2000; Karowe and Grubb, 2011; Mikkelsen et al., 2015b). For instance, increased resistance to potato virus Y (PVY) displayed by tobacco plants under eCO₂ is correlated with an increased accumulation of secondary metabolites such as nicotine and phenylpropanoids (e.g. chlorogenic acid (CGA), 5-O-caffeoyl-D-quinic acid), lignins and coumarins (e.g. scopoline and scopoletin) (Liu et al., 2018; Matros et al., 2006).

Terpenoids are another class of secondary metabolites regulated by

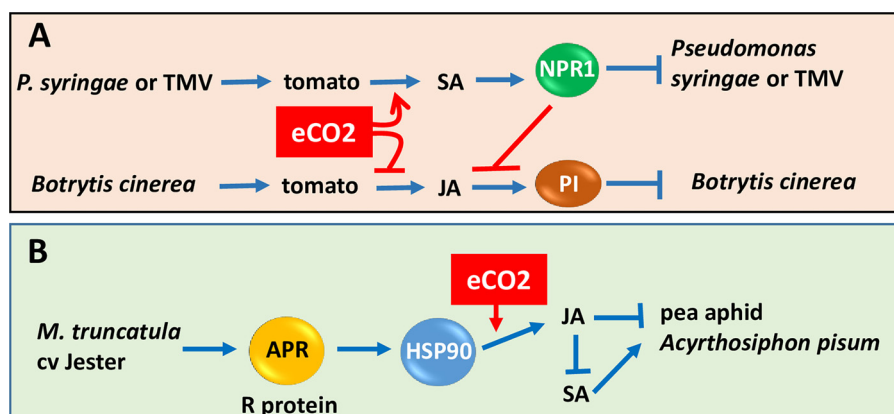


Fig. 5. eCO₂ modulates the crosstalk between SA and JA signalling during host-pathogen interactions.

A) In tomato, eCO₂ promotes disease resistance against and tobacco mosaic virus (TMV) and *Pseudomonas syringae* by promoting SA signalling while eCO₂-mediated suppression of the JA pathway and protease inhibitors (PI) reduce JA-dependent resistance to the necrotrophic fungal pathogen *Botrytis cinerea*. The master regulator NPR1 modulates the antagonistic interaction between SA and JA pathways (Zhang et al., 2015).

B) eCO₂ promotes JA signaling while suppressing the SA pathway in *Medicago truncatula* cv. Jester in an R gene (APR for *Acyrtosiphon pisum* resistance and HSP90)-dependent manner. This reduces aphid feeding activity (Sun et al., 2018).

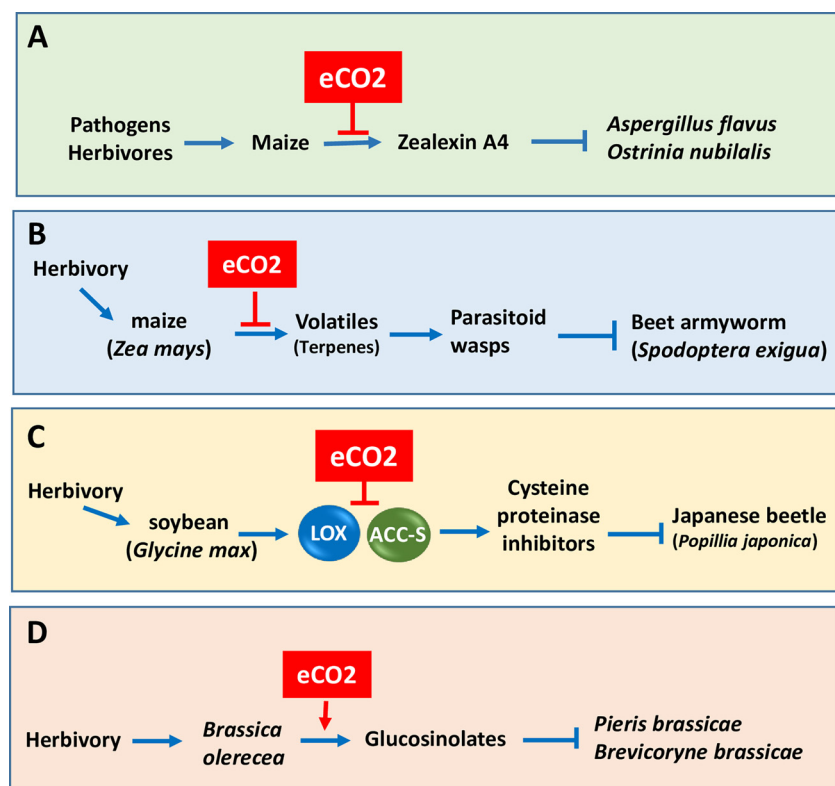


Fig. 6. eCO₂ regulates the production of defence-associated metabolites during plant-parasite interactions.

A) eCO₂ suppresses the production of Zealexin A4 induced by pests and pathogens in maize (Christensen et al., 2018).

B) In maize, eCO₂ suppresses the herbivory dependent production of volatile terpenoids that attract parasitoid wasps (Block et al., 2017).

C) In soybean, eCO₂ suppresses JA/ETH biosynthesis genes encoding a lipoxygenase (LOX) and an amino-cyclopropane-1-carboxylate synthase (ACC-S) involved in the production of cysteine proteinase inhibitors which are toxic to the Japanese beetle (*Popillia japonica*) (Zavala et al., 2009).

D) In *Brassica oleracea*, eCO₂ promotes the production of glucosinolates effective against the herbivorous insects *Pieris brassicae* and *Brevicoryne brassicae* (Klaiber et al., 2013a).

eCO₂ during biotic interactions (Loreto et al., 2001). In maize, eCO₂ suppresses the induction of the sesquiterpenoid metabolite zealexin A4 (ZA4) by the fungal pathogen *Aspergillus flavus* or the herbivorous insect *Ostrinia nubilalis* (Christensen et al., 2018) (Fig. 6A). Indeed, together with earlier findings (Vaughan et al., 2014, 2016b), it appears that eCO₂ has a negative effect on multiple maize defences although additional work is required to determine if down-regulated defences under eCO₂ increase the susceptibility of this species to pest and/or pathogen attack.

In soybean (*Glycine max*), eCO₂ suppresses the expression of genes involved in JA and ethylene biosynthesis such as *LOX7* and *LOX8* and *ACC-S* (amino-cyclopropane-1-carboxylate synthase). The reduced expression from these phytohormone biosynthesis genes in soybean is correlated with suppressed levels of cysteine protease inhibitors (CsyTPIs) and an increased weight gain of the Japanese beetle (*P. japonica*) as CsyTPIs reduce insect growth by inhibiting their gut cysteine activities (Fig. 6C) (Zavala et al., 2009).

Glucosinolates are nitrogen- and sulphur-containing secondary metabolites produced by Brassica species. In response to mechanical damage or herbivory, glucosinolates are converted into toxic compounds that act as insect deterrents. eCO₂ positively regulates glucosinolate levels in a species- and environment-specific manner (Karowe et al., 1997; Schonhof et al., 2007). Under eCO₂, the diamondback larvae (*Plutella xylostella*) induces glucosinolates in *Arabidopsis* although no significant association between glucosinolate levels and insect fitness could be found in this interaction (Bidart-Bouzat et al., 2005). eCO₂ also differentially regulates glucosinolate levels in an herbivory-dependent manner. For instance, in the absence of herbivory, eCO₂ negatively affects the production of indolic glucosinolates in *Brassica napus*. However, when attacked by the herbivorous insect *Plutella xylostella*, eCO₂ promotes the production of indolic glucosinolates in this species (Himanen et al., 2008). eCO₂ reduces the activity of leaf-feeding insect *Pieris brassicae* or the phloem-feeding insect *Brevicoryne brassicae* by promoting glucosinolate production in *B. oleracea* (Klaiber et al., 2013a, Fig. 6D).

Interestingly, pests and pathogens have developed mechanisms to

detoxify host defences (Kettle et al., 2015). eCO₂ has the potential to modify such detoxification mechanisms during plant-biotic interactions. For instance, it has been suggested that eCO₂ compromises indole glucosinolate detoxification mechanisms operating in the specialist herbivore *Pieris rapae* (Landosky and Karowe, 2014).

In soybean, flavonoid (e.g. quercetin) levels increase under eCO₂ in response to the skeletonizing insect *Popillia japonica* but not in response to the chewing insect *Vanessa cardui* or the phloem feeder *Aphis glycines* (O'Neill et al., 2010), suggesting that this response is dependent on the type of attacker. In *Plantago maritima*, eCO₂ causes minor increases in lignification and caffeic acid levels (Davey et al., 2004). In alfalfa (*M. sativa*), saponins, a class of anti-insecticidal defence compounds, show significant increases in response to herbivory under eCO₂ (Agrell et al., 2004). However, if these increases confer enhanced pathogen resistance have not been tested.

9. eCO₂ and host nutritional status

As indicated before, various agronomic practices, the availability of suitable hosts and their nutritional status, the availability of predator species and specific environmental conditions such as high temperatures can also influence the effect of eCO₂ on plant-pest interactions (Gherlenda et al., 2015, 2016; Guerenstein and Hildebrand, 2008; Reddy et al., 2004; Teawkul et al., 2015). In crop plants with C3 photosynthesis, eCO₂ is known to have a positive effect on carbohydrate accumulation and associated increases in plant biomass. However, N levels are not affected by eCO₂. As a result, the C/N ratio, which in turn alters the biosynthesis of secondary metabolites and the palatability of plant tissues to insect attack, increases (reviewed by Sun et al., 2016, 2010b). Indeed, eCO₂-modulated changes in plant's nutritional quality (e.g. reduced N and increased C concentrations or increased C/N ratio) can also alter biotic interactions (Bidart-Bouzat and Imeh-Nathaniel, 2008; Boullis et al., 2015; Ryan et al., 2014; Trebicki et al., 2016; Xie et al., 2015a; Vassiliadis et al., 2016; Ye et al., 2010). It is also possible that some physiological changes induced in the host by parasites under eCO₂ are beneficial to attackers. For instance, the amino acid

metabolism pathway upregulated in *M. truncatula* under eCO₂ promotes the population growth of the pea aphid *A. pisum* (Guo et al., 2013). In addition, eCO₂ seems to affect the trade-off between plant growth and defence by affecting the way that plant resources can be allocated into each of these physiological processes (Sun et al., 2011).

10. Effect of eCO₂ on pathogenicity-related processes

As indicated above, very little is known about the pathogenicity- or herbivory-related processes that are directly or indirectly affected by eCO₂ in pest and pathogen populations. It can be speculated that various parasite traits such as virulence, aggressiveness, fecundity and evolution can be driven at least in part by an altered host physiology under eCO₂ (Liu et al., 2017). It is also possible that eCO₂-mediated alterations in the host stimulate the production of pathogen-derived secondary metabolites and toxins that can function as virulence factors. For instance, under eCO₂, the grains from *Fusarium culmorum*-infected wheat plants contain increased levels of the trichothecene mycotoxin DON (deoxynivalenol), which acts as a pathogenicity factor in most cereal-infecting *Fusarium* pathogens (Bencze et al., 2017). However, it is currently unknown if increased DON levels are resulted from the induction of DON biosynthesis genes as a consequence of direct CO₂ sensing by the pathogen or by the factors produced in the host under eCO₂. In maize, eCO₂ promotes susceptibility to the fungal pathogen *F. verticilloides* without affecting the production of the fungal toxin fumonisin (Vaughan et al., 2014).

Similarly to the differential effects of eCO₂ on different pathogen species, the effect of eCO₂ on different insect species seems to be dependent on the pest species as even closely related insects can display different responses to eCO₂. For instance, the survival rate of the thrip *Frankliniella occidentalis*, a serious pest of vegetables and ornamental species, increases but that of *F. intonsa*, a related species, decreases under eCO₂ (ShuQi et al., 2017).

11. eCO₂ and indirect defence

Indirect defence, attracting the enemies of insect pests by plants releasing volatile signals, plays an integral role in defence against insect pests (Karban et al., 2014). For instance, the volatile terpenoids released by sweet corn attract parasitoid wasps, natural enemies of beet armyworm (*Spodoptera exigua*). eCO₂ suppresses transcript levels of the genes encoding terpene synthases. Maize plants infested with *S. exigua* show reduced emissions of a major sesquiterpene and two homoterpene species under eCO₂ (Fig. 6C). It was speculated that reduced emissions may be resulted not only from the reduced production of terpenes but also impaired mechanisms to release these compounds possibly due to the effects of eCO₂ on stomatal conductance (Block et al., 2017). In Brussels sprout (*B. oleraceae*), eCO₂ reduces volatile emissions but this requires a period of eCO₂ acclimatisation (e.g. 10 weeks of exposure to eCO₂) (Klaiber et al., 2013b). eCO₂ is also known to alter the composition of root exudates that act as signals in recruiting entomopathogenic nematodes, a group of small insects that parasitise plant pathogenic nematodes (Turlings et al., 2012).

12. eCO₂ and chemical communications in insect pests

To protect themselves from natural enemies, social insect species such as aphids release alarm signals that trigger an escape behaviour in insect populations (Boullis et al., 2016). eCO₂ alters the escape behaviour of aphids by affecting their ability to communicate chemically with one another using such signals and therefore this has the potential to affect predator-prey interactions (Boullis et al., 2017; Sun et al., 2010a). eCO₂ suppresses both the production and the release of (E)- β -farnesene (E β f), a pheromone used by the pea aphid (*Acyrtosiphon pisum*) as an alarm or escape signal (Boullis et al., 2017). A reduced sensitivity of the aphid *Amphorophora idaei* to E β f results in enhanced

predation by the ladybird (*Harmonia axyridies*) larvae (Hentley et al., 2014). A similar suppressive effect of eCO₂ on E β f was also observed for the grain aphid *Sitobion avenae* (Sun et al., 2010b).

13. Interactions between eCO₂ and other environmental factors during plant-biotic interactions

The effect of eCO₂ on plant-biotic interactions may be modified by various intrinsic and extrinsic factors such as individual plant species and genotypes (e.g. C3 vs. C4 species; monocots vs dicots) and a number of environmental factors such as elevated temperatures, ozone, drought and nutrient levels (Aguilar et al., 2015; Casteel et al., 2008; Chung et al., 2017; Coviella et al., 2000; Del Toro et al., 2015, 2017; Fleischmann et al., 2010; Gao et al., 2008; Huot et al., 2017; Jamieson et al., 2012; Johnson et al., 2014; Johnson and Hartley, 2017; Koo et al., 2016; Mikkelsen et al., 2015a; Mitchell et al., 2003; Niu et al., 2016; Niziolek et al., 2013; O'Neill et al., 2011; Plessl et al., 2007; Ryan et al., 2014; Robinson et al., 2012; Terrer et al., 2018; Vega-Mas et al., 2017; Zhang et al., 2017). During soybean-Japanese beetle (*Popillia japonica*) interactions, eCO₂ suppresses the JA pathway and this increases the susceptibility of soybean to the beetle. However, water stress experienced during this time negates the negative effects of eCO₂ on JA signalling, abolishing eCO₂-mediated susceptibility to the Japanese beetle (Casteel et al., 2012b). In contrast, eCO₂-mediated susceptibility to the stalk rot pathogen *F. verticilloides* increases under drought stress in maize (Vaughan et al., 2016b). These examples indicate that the same stress factor can differentially affect different biotic interactions under eCO₂.

Wounding is known to induce the JA pathway and the levels of glucosinolates, which themselves are JA-inducible. However, under eCO₂, the so-called JA-burst or rapid activation of the JA pathway, and the production of glucosinolates, is suppressed in wounded plants grown in a high nitrate environment (Paudel et al., 2016). Although the reason(s) for this phenomenon is not clear, one possibility proposed by the authors of this study is that reduced photorespiration suppresses NADPH levels required for nitrate assimilation in C3 plants under eCO₂, subsequently affecting the cellular redox balance and the ability of the host plant to respond to stresses (Paudel et al., 2016). The levels of secondary metabolites are also affected by interactions between eCO₂ and abiotic stress factors such as high temperatures and drought during plant-biotic interactions in a species- and attacker-dependent manner (Kuokkanen et al., 2001; Ode et al., 2014; Pérez-López et al., 2017; Vaughan et al., 2016b). In addition, eCO₂ alters host preferences (cotton *Gossypium hirsutum* vs. alfalfa *Medicago sativa*) of the moth *Spodoptera littoralis* in a manner that is also dependent on whether the plants were damaged or not prior to insect infestation (Agrell et al., 2006).

14. eCO₂ and tritrophic plant-parasite interactions

eCO₂ also has the potential of influencing the so-called “tritrophic” interactions involving three partners (e.g. plant-insect-predator, plant-insect-virus or plant-mutualistic microbe-virus) (Castex et al., 2017; Dyer et al., 2013; Fu et al., 2010; Rúa et al., 2013). For example, plant viruses are transmitted by sap-sucking insects such as aphids. Therefore, the effect of eCO₂ on plant viruses can be closely linked to the aphid behaviour. eCO₂ promotes the ability of aphids (e.g. *Myzus persica*) to transmit viruses (e.g. Cauliflower Mosaic Virus or CMV) in pepper (Dáder et al., 2016) and Potato virus Y (PVY) in tobacco (Bosquee et al., 2018). eCO₂ causes a significant increase in the incidence of Barley Yellow Dwarf Virus (BYDV) infection in wheat in multi-year FACE (Free Air CO₂ Enrichment) as well as glasshouse trials (Trebecki et al., 2015, 2017b) although the potential roles of insect vectors in this phenomenon remain elusive.

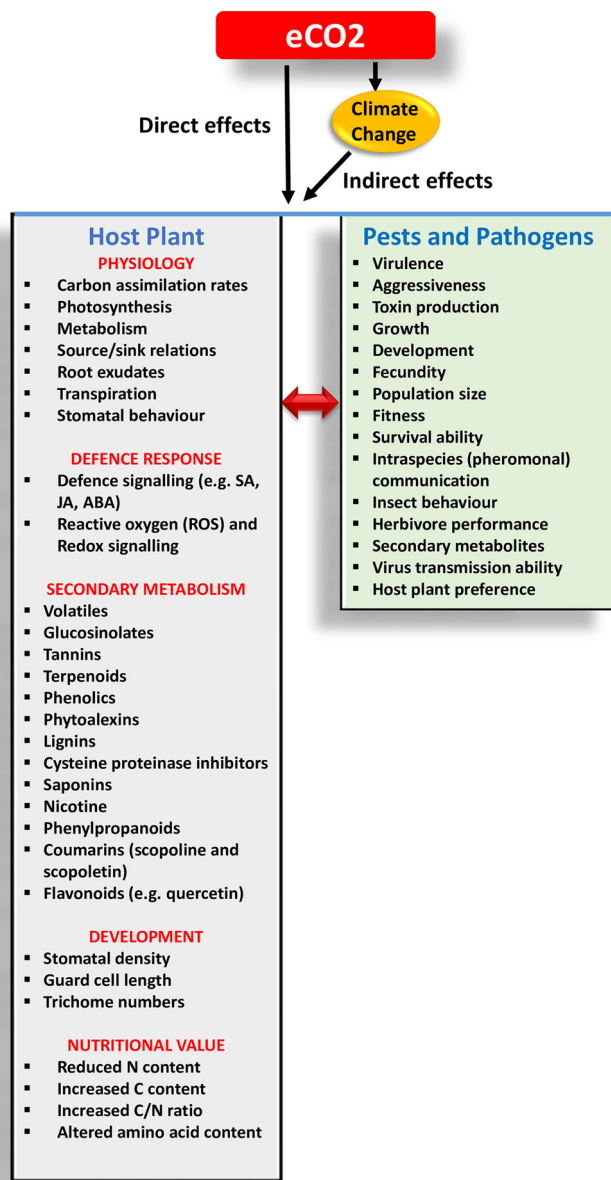


Fig. 7. Elevated CO₂ (eCO₂) directly or indirectly affect multiple host and parasite traits during their interactions. Indirect effects of eCO₂ are attributed to the contribution of this gas to climate change.

15. Conclusions and future prospects

Recent studies reviewed in this paper indicate that potential effects of eCO₂ on plant-biotic interactions can be complex and potentially vary from one interaction to another. A summary of eCO₂-mediated effects discussed in this review is presented in the model given in Fig. 7. Although most studies reviewed here have focussed on relatively direct effects of eCO₂ on plant-parasite interactions, it is clear that eCO₂-mediated climatic changes can also have a significant impact on various environmental factors affecting plant pest and pathogen resistance (Fig. 7). Furthermore, so far, most studies in this area have focussed on the host side of the interaction while relatively little is known how eCO₂ might affect pest and pathogen biology.

Genome-wide analyses of plant and/or parasite gene expression during plant-biotic interactions could help identify new plant and/or pathogen processes influenced by eCO₂ (Jauregui et al., 2015; Liu et al., 2014; Powell et al., 2017). However, surprisingly only few transcriptome studies have so far been conducted to dissect plant-biotic

interactions under eCO₂. A recent study showed that eCO₂ alters the transcriptome of *Eucalyptus grandis* roots during their interactions with mycorrhiza (*P. microcarpus*). In addition, eCO₂ differentially affects the interaction between *E. grandis* and promotes increased colonisation of roots in an isolate-dependent manner (Plett et al., 2015). Integrating data from multiple omics platforms (transcriptome, proteome and metabolome), as was done recently to dissect abiotic stress responses under eCO₂ (Zinta et al., 2018), would reveal new insights into how plants and parasites adapt to changes at atmospheric CO₂ levels (Liu et al., 2016).

Non-photosynthetic parasitic plants and weeds cause significant crop losses. eCO₂ is known to promote weed growth (Anderson and Cipollini, 2013; Jabran and Doğan, 2018) and thus can potentially alter the competition between weeds and crops (Larson et al., 2018; Ramesh et al., 2017). One recent study suggested that eCO₂ can cause weeds to acquire resistance to the widely used herbicide glyphosate (Fernando et al., 2016). In contrast, another study showed that eCO₂ promotes weed growth without altering the efficacy of glyphosate action (Jabran and Doğan, 2018). Additional studies are required to assess the effects of eCO₂ on crop-weed or crop-parasitic plant interactions.

So far, the impact of eCO₂ on plant health has been assessed mainly by scoring disease symptom development (Bencze et al., 2013; Chittarra et al., 2015). Although the damage caused to photosynthetic tissues by pests and pathogens can negatively affect crop yields, estimating crop losses based on lesion development may not be a reliable indicator of overall losses as eCO₂ can promote crop yields and thereby compensate potential yield losses. For instance, the negative effect of root-herbivory observed under aCO₂ on plant belowground biomass could not be observed under eCO₂ (McKenzie et al., 2016). Therefore, wherever possible, yield data from field (e.g. FACE) trials may be needed to draw reliable conclusions about the effects of eCO₂ on crop losses due to pests and pathogens.

The majority of plant-biotic interactions that have been investigated thus far under eCO₂ affects above-ground plant parts. A number of pests and pathogens are soil-borne and interact with plants through the roots (De Coninck et al., 2015). CO₂ is a ubiquitous signal emitted from plant roots and relatively low CO₂ concentrations are known to attract root-feeding arthropods (reviewed by Hiltbold and Turlings, 2012). It is, therefore, possible that eCO₂ alters the communication between plant roots and parasitic or beneficial/symbiotic soil microorganisms (Bertrand et al., 2007; Kivlin et al., 2013; Rogers et al., 2009). Indeed, eCO₂ influences the composition of soil microbial communities by altering the production of root exudates (Calvo et al., 2017; Gschwendtner et al., 2015; Hayden et al., 2012; Johnson and Riegler, 2013; Lipson et al., 2014; Wang et al., 2017), which in turn directly or indirectly influence plants' response to pests and pathogens (Schenk et al., 2012). eCO₂ also compromises the resilience of soil microbes to extreme seasonal droughts expected to be occurring more frequently under climate change (Drigo et al., 2017). The effect of eCO₂ on soil microbes can also be influenced by soil types (Procter et al., 2014).

How eCO₂ would affect transgene expression if transgenic plants were widely employed against pests and pathogens in the future is another area that requires further investigation. One recent study suggested that eCO₂ promotes the expression of the *Bacillus thuringiensis* Bt toxin gene conferring resistance to lepidopteran pests in cotton under relatively high nitrogen levels (Jiang et al., 2017).

In conclusion, recent studies reviewed here have revealed many new insights into the complexities associated plant-biotic interactions under eCO₂. Future studies will be of critical importance to mitigate potentially deleterious effects of eCO₂ on plant-biogenic interactions and to breed new varieties that will perform well under eCO₂.

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